

Composition and richness of the ichthyofauna in a *terra firme* forest stream of the Colombian Amazonia

by

F. Arbeláez, G. Gálvis, J.I. Mojica & S. Duque

Fernando Arbeláez, Prof. Dr. Germán Galvis & Prof. Dr. José Iván Mojica, Ichthyology Laboratory, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Ciudad Universitaria Cr. 30 Cl. 45, Bogotá D.C., Colombia; e-mail: ferarbe@hotmail.com
Prof. Dr. Santiago Duque, IMANI, Universidad Nacional de Colombia, Leticia, Colombia; e-mail: ferarbe@cable.net.co

(Accepted for publication: May, 2004).

Abstract

An intensive inventory of the ichthyofauna in a small *terra firme* forest stream of the Colombian Amazonia was carried out to examine the ichthyological composition of these environments and to identify patterns of fish species permanency during the seasonal cycle. One hundred and nine fish species were collected, which is the highest recorded number of species for this kind of environments in the Amazonia. Richness estimators showed that more than 87 % of the estimated species have been captured. Permanency analyses indicated that 44 species were permanent and only six species were seasonal, suggesting a low seasonal variation of the species composition during the year. Finally, high species richness is discussed in relation to key ecological factors such as productivity, habitat heterogeneity, climatic variability, harshness, environmental age and biogeographic area.

Keywords: **Ichthyology, igarapé, ecology, inventory, richness factors.**

Resumo

Realizou-se um inventário intensivo da ictiofauna de um pequeno curso de água numa pequena floresta de *terra firme* na Amazônia colombiana, de modo a examinar a composição ictiológica destes ambientes e identificar padrões de permanência das espécies piscícolas durante o ciclo sazonal. Foram recolhidas cento e nove espécies de peixes, o que representa o maior número de espécies registado para este tipo de ambientes na Amazônia. Estimadores da riqueza mostraram que mais de 87 % das espécies estimadas foram capturadas. Análises de permanência indicaram que 44 espécies são permanentes e apenas seis espécies são sazonais, sugerindo uma baixa variação sazonal da composição específica durante o ano. Finalmente, a elevada riqueza específica é discutida em relação a factores ecológicos chave como produtividade, heterogeneidade do habitat, variabilidade climática, adversidade, idade ambiental e área biogeográfica.

Introduction

Terra firme forest streams (Igarapés) are unique among Amazonian freshwater systems. In contrast to the aquatic systems that are directly influenced by the hydric pulses of the major rivers, the water level of *terra firme* forest streams depends exclusively on local

storm events (FORSBERG et al. 2001; GOULDING et al. 2003). Furthermore, these streams drain poor and extremely leached forest soils, which results in highly acidic water, very low nutrient and dissolved solid concentration, and the presence of certain organic compounds that confer it a distinctive dark colour (LOWE-McCONNEL 1987). Despite the lack of abundant primary productivity, significant allochthonous contribution from the surrounding forest allows the development of a well-structured fish community (ARBELÁEZ 2000; KNÖPPEL 1970; LOWE-McCONNEL 1987).

In aquatic systems directly influenced by major rivers, water level, resource availability and physicochemical conditions vary seasonally, periodically changing the structure of fish assemblages (e.g. richness, composition and abundance) (GOULDING et al. 1988, 2003; HENDERSON & ROBERTSON 1999; PRIETO 2000; VAL & DE ALMEIDA-VAL 1995). In contrast, the less variable limnological characteristics of *terra firme* streams result in a more temporally stable structure (BÜHRNHEIM & COX-FERNANDES 2001).

Despite the nutrient poverty and acidity of their water, forest streams have a high richness of fish species (CRAMPTON 1999; KNÖPPEL 1970; LOWE-McCONNEL 1975; SAUL 1975). Although they have economic importance as ornamentals (CHAO 2001), little is known about the long-term composition and permanency of forest stream fish species.

The aim of this study was twofold: first, to characterize the composition of the fish community as completely as possible; and second, to analyse the permanency of these species during the year. This is an important step towards furthering our knowledge about population ecology and biodiversity in these systems, and may have key implications for their conservation.

Material and methods

Study area

The study was conducted near the city of Leticia, Colombia, located in the northern bank of the Amazon River (04°9'S, 69°57'W, elevation 84 m). The region is on the ITCZ, which determines a monomodal precipitation regime. Mean annual precipitation is 3404 mm (1984 to 1998 average), with the rainy season occurring between December and April and the driest season between June and August (however, rains occur throughout the year). Precipitation regime during the year of the study (1999) was atypical due to El Niño and La Niña events and rains were not clearly monomodal, with a very marked peak occurring in May.

La Arenosa (4°07'24''S, 69°57'05''W) is a small *terra firme* stream that runs through a relatively undisturbed tract of forest from the forest interior to a floodplain of the Amazon River (Fig. 2). Fishing was carried out in a small clear area surrounded by dense forest. At the sampling site, the stream is not dammed by the level of the Amazon River during high waters, as is the case near the outlet. Stream width ranges from 2-5 m and depth is <2 m in its deepest parts. Water velocity is ca. 0.15m·s⁻¹. Storms, which are more frequent during the rainy season, produce fast but transient increases in stream water level and velocity, resulting in the flooding of adjacent areas. (ARBELÁEZ 2000).

La Arenosa drains very poor soils from alluvial plains of tertiary Amazonian blackwater rivers (DUKE & NÚÑEZ 1997). The water has low pH (5.51-6.01, $\xi=5.78$), very low conductivity (18-38 $\mu\text{S}\cdot\text{cm}^{-1}$, $\xi=30.62 \mu\text{S}\cdot\text{cm}^{-1}$), relatively high dissolved oxygen⁻¹ (70 % of saturation), intermediate temperatures ($\xi=25^\circ\text{C}$), high transparency (Secchi disc always visible) and a characteristic blackish colour (ARBELÁEZ 2000).

Sampling methods and data analysis

Ichthyological studies in complex tropical communities offer special methodological challenges due to the

high number of species and habitat heterogeneity. Although the use of multiple fishing arts may decrease the accuracy of abundance-based analyses and diversity estimators, it increases the possibility of sampling the complete fish community (HENDERSON & ROBERTSON 1999). In this study, the ichthyological composition of a *terra firme* forest stream in the Colombian Amazonia was examined through an intensive inventory carried out using multiple fishing arts. Therefore, richness estimators and analyses were based in the presence and absence of species and not in their abundance and diversity. Three main six-day fishing campaigns were carried out in late April (high precipitation, rising waters), early July (low precipitation, decreasing waters) and November (early rainy season, low waters) to identify patterns of fish permanency during contrasting periods of the seasonal cycle. Additional samples were obtained during shorter surveys in January, June, August and October to complement the taxonomic inventory, totalling 32 fishing days. Fishing was conducted from 16h to 20h along a 200 m tract of stream, attempting to include all possible fish microhabitats. Multiple fishing methods were used for sampling: throwing nets (2 to 4 m diameter x 0.5 to 2 cm mesh), seine nets (1 to 2.5 m x 3 to 12 m x 0.1 to 0.5 cm mesh) and gill nets (15 m x 2 m x 1 to 3 cm mesh). Captured individuals were fixed in formol (10 %), identified, preserved in ethanol (70 %) and deposited in the ichthyology collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN numbers in table 1). The validity of the taxonomic identification was confirmed in FishBase (FROESE & PAULI 2003). The inventory was compared with the preliminary checklist of fish species for the Colombian Amazonia (MOJICA 1999), to verify new reports in the area.

Species richness was estimated using EstimateS 6.0b software (COLWELL 2000). Incidence-based richness estimators such as ICE (Incidence-based Coverage Estimator), Chao 2 (Incidence-based Chao estimator), Jack 1 and Jack 2 (First-order and Second-order Jackknife estimators) and Bootstrap (incidence-based) were analysed by configuring the software to make 1000 randomisations of the samples without replacement.

Species permanency was determined through their presence or absence during the three major sampling campaigns. Species were classified as permanent (P), frequent (F) or seasonal (S), according to their presence in three, in two or in one of the surveys, respectively. Species that were collected with only one or two individuals were considered as "rare", and were not included in permanency analysis to avoid over-estimation of frequent and seasonal species (GREEN 1979).

Results

The fish community of La Arenosa was found to be composed of 109 species belonging to 7 orders and 27 families (Table 1). The dominant taxonomic orders (by number of species) were Characiformes (54 %, 59 spp.), Siluriformes (22 %, 24 spp.), Perciformes (13 %, 15 spp.) and Gymnotiformes (7 %, 8 spp.). The families with the highest richness were Characidae (31 %, 34 species), Cichlidae (13 %, 14 spp.) and Loricariidae (7 %, 8 spp.). Fifty-two of the species were new reports for the Colombian Amazonia. This number includes both confirmed species and unconfirmed species (*cf.* and *sp.*) belonging to genera previously unreported for the area, and it is therefore likely to increase as confirmation of the taxonomy of some species continues.

Incidence-based richness was estimated as ranging from 115.92 (Chao estimator) to 124.5 species (First order Jackknife, SD = 4.4) (Table 2). Thus, the observed number of species is between 87.6 % and 94.0 % of the estimated number.

Permanency analysis indicated that out of the 99 species captured during the major surveys (ten other species were captured during the supplementary samplings), 44 species were permanent, 16 frequent and, only 6 seasonal. The remaining 33 species were represented by only one or two individuals were not considered in the analyses.

Discussion

This work reports the highest number of species recorded for Amazonian forest streams compared to other published studies (Table 2). Rather than indicating an unusual ichthyological richness of the Colombian Amazonia, this might reflect the effectiveness of using multiple sampling techniques, the length of our survey and the diversity of habitats sampled. The use of a single sampling method, such as ichthyocides (e.g; CASTRO & CASATTI 1997; KNÖPPEL 1970; SAUL 1975), allows for abundance-based and diversity analyses but reduces the range of the inventory, since rotenone has variable effectiveness depending on the species and population size (PREJS & COLOMINE 1981). The high number of unreported species found in this study further highlights the limited knowledge about Colombian ichthyological biodiversity.

The abundance of resident species and low seasonal compositional variation found in this study are common in Amazonian forest streams (e.g. BÜHRNHEIM & COX-FERNANDES 2001), probably as a result of a reduced seasonality in resource availability and environmental conditions. In contrast, the seasonal variability of fish communities in Amazonian hydric pulse systems is well-established (GOULDING et al. 1988, 2003; LOWE-McCONNELL 1975; VAL & DE ALMEIDA-VAL 1995). Permanency analyses in Yahuaraca Lake, an Amazon River floodplain 10 km away from La Arenosa (SANTOS-ACEVEDO 2000; VEJARANO 2000), confirmed the existence of similar patterns, suggesting that water level seasonality involves significant changes in the physicochemical conditions and resource availability.

The ichthyological richness of La Arenosa is far greater than in larger tropical rivers such as the Ganges, Congo, Niger (KNÖPPEL 1970), Atrato, Cauca and Catatumbo (GALVIS et al. 1997). This is remarkable, considering its comparatively extremely small drainage basin (<10 Km²). Morphological features such as miniaturization, as well as a wide range of feeding and reproductive strategies found in the ichthyofauna of La Arenosa (ARBELÁEZ 2000), suggest that high richness is probably a result of adaptative processes to reduce inter and intra specific competition, to maximize resources allocation and to allow a greater overlap of niche breadths (TOWSEND et al. 2003). A number of key environmental and historical factors that may also account for the high ichthyological richness in stream ecosystems (TOWSEND et al. 2003): productivity, habitat heterogeneity, environmental harshness, climatic variability, environmental age and biogeographic area are discussed below.

1. Productivity. Richness seems to be directly related to the range of available resources and not to the supply rates of the resources (TOWSEND et al. 2003). The constant contribution of organic matter and terrestrial organisms in Amazonian forest streams supports a wide range of allochthonous and autochthonous resources (ARBELÁEZ 2000; KNÖPPEL 1970; WALKER 2001), despite the fact that the supply rate of these resources is limited, compared to more productive environments like the várzea (LOWE-McCONNELL 1975).

2. Habitat heterogeneity. Environmental heterogeneity provides a greater variety of microhabitats and microclimates, more places to hide from predators, etc. (LOWE-McCONNELL 1975; TOWSEND et al. 2003). A wide array of habitats (open waters, sandy or loamy bottoms, fallen trunks, sub-aquatic roots, caves, holes and variable current speeds, littoral slopes and depth) such as those found in La Arenosa are ideally suited for the development of many tropical fish populations (BÜHRNHEIM & COX-FERNANDES 2003; FORSEBERG et al. 2001).

3. Environmental harshness. Extreme environmental conditions commonly provide habitat for specialized organisms and are conducive to reduced species richness (TOWSEND et al. 2003). Due to the input of allochthonous materials in La Arenosa, factors like low pH and low concentration of dissolved solids, which may reduce primary productivity, do not seem to restrict fish species richness (KNÖPPEL 1970; LOWE-McCONNEL 1975).

4. Climatic variability. Unpredictable but moderate climatic changes may foster species richness by maintaining population below their carrying capacity, reducing inter-specific competition and the possibility of competitive exclusion (TOWSEND et al. 2003). Water level changes in La Arenosa, although swift and unpredictable, are neither drastic nor prolonged, creating a mild seasonality of environmental conditions and resource availability that allows for little seasonal variation of the fish assemblages (BÜHRNHEIM & COX-FERNANDES 2001).

5. Environmental age. Prolonged evolutionary time of a community has been suggested as a factor determining high species richness (LOWE-McCONNEL 1975; TOWSEND et al. 2003). Blackwater rivers and their fish communities have had longer evolutionary histories than sediment-rich systems in Amazonia, because they have existed prior to the raising of the Andes (VAL & DE ALMEIDA-VAL 1995). Although La Arenosa is not a blackwater system *sensu stricto*, its similar physicochemical characteristics allow it to sustain the rich ichthyofauna of blackwater rivers.

6. Biogeographic area. Large biogeographic areas can host a high number of species due to multiplicity of habitats, high rates of immigration and speciation by effect of the area *per se*, or both (TOWSEND et al. 2003; TRIANTIS et al. 2003). The Amazonian forest has a surface area of nearly 7.000.000 km², of which at least 1.000.000 km² correspond to *terra firme* aquatic systems (GOULDING et al. 2003). This complex web of streams, canals and swamps represent an extensive and heterogeneous area for colonization and diversification of fish species.

The conjunction of all these factors results in what is probably one of the aquatic systems with the highest richness of fish species per area in the world. Our research has underlined the importance of maximizing the inventory coverage by using multiple fishing methods, sampling across seasons, covering a wide range of microhabitats and hours of fish activity, and collecting every captured individual. The high number of resident species found in La Arenosa suggests that *terra firme* environments are relatively independent of the hydric pulse of the major rivers, which is commonly considered as the most important ecological factor in Amazonian hydrological systems.

Acknowledgments

This work was possible thanks to the financial support of the CYTED of Spain, to the equipment and the ichthyology laboratory of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia and to the logistical support of the Instituto de Investigaciones Amazónicas-IMANI, Universidad Nacional de Colombia, in Leticia.

Thanks to Carlos Granado, Universidad de Sevilla, and Javier Lobón, Museo de Historia Natural de Madrid, Spain for their support; also to our colleagues, Silvia Vejarano, Marisol Santos and Edgar Prieto; to Gabriel Aricari for his field guidance, to Javier Maldonado for his aid with the taxonomy of Gymnotiformes, to Natalia Ruiz, Roxana Yockteng and Alejandro Guarán for their comments on earlier drafts, and in general to all those who made it possible.

References

- ARBELÁEZ, F. (2000): Estudio de la ecología de los peces en un caño de aguas negras amazónicas en los alrededores de Leticia (Amazonia colombiana). - B.Sc.-thesis, Universidad Nacional de Colombia, Bogotá, Colombia.
- BÜHRNHEIM, C.M. & C. COX-FERNANDES (2001): Low seasonal variation of fish assemblages in Amazonian rain forest streams. - *Ichthyol. Explor. Freshwaters*. **12**(1): 65-78.
- BÜHRNHEIM, C.M. & C. COX-FERNANDES (2003): Structure of fish assemblages in Amazonian rain-forest streams: effects of habitats and locality. - *Copeia* **2003**(2): 255-362.
- CASTRO, R.M. & L. CASATTI (1997): The fish fauna from a small forest stream of the upper Paraná River basin, southeastern Brazil. - *Ichthyol. Explor. Freshwaters* **7**(4): 337-352.
- CHAO, N.L. (2001): The fishery, diversity and conservation of ornamental fishes in the Rio Negro Basin, Brazil. A review of Project Piaba (1989-99). - In: CHAO, N.L., PETRY, P., PRANG, G., SONNESCHIEN, L. & M. TLUSTY (eds.): Conservation and management of ornamental fish resources of the Rio Negro basin, Amazonia, Brazil - Project Piaba: 161-240. EDUA, Manaus.
- COLWELL, R.K. (2000): EstimateS: Statistical estimation of species richness and shared species from samples. Version 6.0b1. - User's Guide and application published online at <http://vice-roy.eeb.uconn.edu/estimates>.
- CRAMPTON, W.G.R. (1999): Os peixes da reserva Mamirauá: diversidade e história natural na planície alagável da Amazônia. - In: QUEIROZ, H.L. & W.G.R. CRAMPTON (eds.): Estratégias para manejo de recursos pesqueiros em Mamirauá: 10-36. Sociedade Civil, Mamirauá & CNPq/MCT, Brasília.
- DUQUE, S.R. & M. NÚÑEZ (1997): Ficoflora de algunos ambientes acuáticos de la Amazonia colombiana. - *Caldasia* **19**(1-2): 279-284.
- FORSBERG, B.R., DIAZ-CASTRO, J.G., CARGNIN-FERREIRA, E. & A. ROSENQVIST (2001): The structure and function of the Negro River ecosystem: insights from the Jaú Project. - In: CHAO, N.L., PETRY, P., PRANG, G., SONNESCHIEN, L. & M. TLUSTY (eds.): Conservation and management of ornamental fish resources of the Rio Negro basin, Amazonia, Brazil - Project Piaba: 125-144. EDUA, Manaus.
- FROESE, R. & D. PAULY (2003): FishBase. Version 27 January 2004. - Accessed online at <http://www.fishbase.org>.
- GALVIS, G., MOJICA, J.I. & M. CAMARGO (1997): Peces del Catatumbo. Asociación Cravonorte, Bogotá.
- GOULDING, M., BARTHEM, R. & E.G. FERREIRA (2003): The Smithsonian atlas of the Amazon. - Smithsonian books, Washington D.C.
- GOULDING, M., CARVALHO, M.L. & E.G. FERREIRA (1988): Rio Negro: rich life in poor water. - SPB Academic Publishing, The Hague.
- GREEN, R. (1979): Sampling design and statistical methods for environmental biologists. - John Wiley & Sons, New York.
- HENDERSON, P.A. & B.A. ROBERTSON (1999): On structural complexity and fish diversity in an Amazonian floodplain. - In: PADOCH, C., AYRES, J.M., PINEDO-VASQUEZ, M. & A. HENDERSON (eds.): Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. Section 1: Fish and Fisheries: 45-58. The New York Botanical Garden Press (NYBG), New York.
- KNÖPPEL, H. (1970): Food of Central Amazonian fishes. Contribution to the nutrient-ecology of Amazonian rain-forest-streams. - *Amazoniana* **2**(3): 257-351.
- LOWE-McCONNELL, R.H. (1975): Fish communities in tropical freshwaters. Their distribution, ecology and evolution. - Longman, New York.
- LOWE-McCONNELL, R.H. (1987): Ecological studies in tropical fish communities. - Cambridge Univ. Press, New York.
- MOJICA, I. (1999): Lista preliminar de las especies de peces dulceacuicolas de Colombia. - Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. **23** (Suplemento Especial): 547-566.

- PREJS, A. & G. COLOMINE (1981): Métodos para el estudio de los alimentos y las interrelaciones tróficas de los peces. - Universidad Central de Venezuela y Universidad de Varsovia, Polonia & Caracas.
- PRIETO, E. (2000): Estudio ictiológico de un caño de aguas negras en la Amazonía colombiana, Leticia - Amazonas. - B.Sc.-thesis. Universidad Nacional de Colombia, Bogotá, Colombia.
- SANTOS-ACEVEDO, M. (2000): Aspectos ecológico de la fauna ictica dominante en la laguna de Yahuaraca, Leticia. - B.Sc.-thesis. Universidad Nacional de Colombia, Bogotá, Colombia
- SAUL, W. (1975): An ecological study of fishes at a site in upper Amazonian Ecuador. - Readings of the Academy of Natural Sciences of Philadelphia **127**(12): 93-134.
- TOWSEND, C., BEGON, M. & J. HARPER (2003): Essentials of ecology. Second edition. - Blackwell, Malden.
- RIANTIS, K.A., MYLONAS M., LIKA K. & K. VARDINOYANNIS (2003): A model for the species-area-habitat relationship. - J. Biogeogr. **30**(1): 19-27.
- VAL, A.L. & V.M.F. DE ALMEIDA-VAL (1995): The fishes of the Amazon and their environment. Springer, Berlin.
- VEJARANO, S. (2000): Ictiofauna de la laguna Yahuaraca y aspectos tróficos y reproductivos de cinco especies predominantes, Leticia-Colombia.- B.Sc.-thesis. Universidad Nacional de Colombia, Bogotá.
- WALKER, I. (2001): Maintenance of biodiversity in the benthic fauna of an Amazonian forest stream. - In: CHAO, N.L., PETRY, P., PRANG, G., SONNESCHIEN, L. & M. TLUSTY (eds.): Conservation and management of ornamental fish resources of the Rio Negro basin, Amazonia, Brazil - Project Piaba: 145-160. EDUA, Manaus.

Table 1: List of captured species in La Arenosa Stream and catalog number. *Species permanency: P = permanent (in three sampling periods), F = frequent (in two periods), S = seasonal (in one period). R = rare species (one or two individuals), A = captured during the supplementary samplings. **New reports for Colombian Amazonia.

Cat. No.	Species	*
Characiformes		
Anostomidae		
ICN 4990	<i>Leporinus agassizi</i> STEINDACHNER 1876	R
ICN 5009	<i>Leporinus friderici friderici</i> (BLOCH 1794)	P
ICN 5282	<i>Rhytiodus microlepis</i> KNER 1859	A
ICN 5019	<i>Schizodon fasciatus</i> SPIX & AGASSIZ 1829	R
Acestrorhynchidae		
ICN 4977	<i>Acestrorhynchus falcirostris</i> (CUVIER 1819)	R
ICN 4934	<i>Acestrorhynchus lacustris</i> (LÜTKEN 1875)**	P
ICN 4932	<i>Acestrorhynchus microlepis</i> (SCHOMBURGK 1841)	F
Characidae		
ICN 4945	<i>Astyanax abramis</i> (JENYNS 1842)**	P
ICN 4986	<i>Axelrodia stigmatias</i> (FOWLER 1913)**	P
ICN 4999	<i>Bryconops (creatochanes)</i> sp. GÜNTHER 1864**	P
ICN 5014	<i>Ctenobrycon hauxwellianus</i> (COPE 1870)	P
ICN 5310	<i>Gymnocorymbus</i> sp. EIGENMANN 1908	F
ICN 5000	<i>Hemigrammus analis</i> DURBIN 1909**	P
ICN 4961	<i>Hemigrammus belottii</i> (STEINDACHNER 1882)	P
ICN 4988	<i>Hemigrammus luelingi</i> GÉRY 1964	R

ICN 4962	<i>Hemigrammus ocellifer</i> (STEINDACHNER 1882)	P
ICN 4931	<i>Hemigrammus schmardae</i> (STEINDACHNER 1882)**	P
ICN 5311	<i>Hyphessobrycon copelandi</i> DURBIN 1908	F
ICN 4923	<i>Jupiaba anteroides</i> (GÉRY 1965)**	R
ICN 4956	<i>Knodus moenkhausii</i> (EIGENMANN & KENNEY 1903)**	P
ICN 4982	<i>Microschemobrycon geisleri</i> GÉRY 1973**	P
ICN 4957	<i>Moenkhausia comma</i> EIGENMANN 1908**	P
ICN 4948	<i>Moenkhausia lepidura</i> (KNER 1858)**	P
ICN 4994	<i>Moenkhausia megalops</i> (EIGENMANN 1907)**	S
ICN 4939	<i>Moenkhausia melogramma</i> EIGENMANN 1908**	P
ICN 4992	<i>Moenkhausia naponis</i> BÖHLKE 1958**	R
ICN 4953	<i>Moenkhausia sanctaefilomenae</i> (STEINDACHNER 1907)	P
ICN 5284	<i>Triportheus angulatus</i> (SPIX & AGASSIZ 1829)	A
Characidae (Bryconinae)		
ICN 5015	<i>Brycon melanopterus</i> (COPE 1872)	R
Characidae (Characinae)		
ICN 4987	<i>Charax leticiae</i> LUCENA 1987	S
ICN 4973	<i>Charax tectifer</i> (COPE 1870)**	P
ICN 5010	<i>Cynopotamus amazonus</i> (GÜNTHER 1868)	S
ICN 4952	<i>Phenacogaster</i> sp. EIGENMANN 1907**	P
ICN 4991	<i>Roeboides myersi</i> (GILL 1870)	R
Characidae (Glandulocaudinae)		
ICN 5023	<i>Gephyrocharax</i> sp. EIGENMANN 1912**	F
ICN 5003	<i>Glandulocauda</i> (cmpj) sp. EIGENMANN 1911	P
ICN 4950	<i>Tytocharax cochui</i> (LADIGES 1950)**	P
Characidae (Iguanodectinae)		
ICN 4985	<i>Iguanodectes spilurus</i> (GÜNTHER 1864)**	R
Characidae (Serrasalminae)		
ICN 4941	<i>Serrasalmus rhombeus</i> (LINNAEUS 1766)	F
Characidae (Tetragonopterinae)		
ICN 5001	<i>Tetragonopterus argenteus</i> CUVIER 1816	P
Crenuchidae (Characidiinae)		
ICN 5002	<i>Characidium zebra</i> EIGENMANN, 1909**	F
ICN 4978	<i>Characidium pellucidum</i> EIGENMANN 1909	F
ICN 4974	<i>Klausewitzia</i> sp.1 GÉRY 1965**	R
ICN 5016	<i>Klausewitzia</i> sp.2 GÉRY 1965**	A
Crenuchidae (Crenuchinae)		
ICN 4949	<i>Crenuchus spilurus</i> GÜNTHER 1863**	P
Ctenoluciidae		
ICN 4976	<i>Boulengerella maculata</i> (VALENCIENNES 1850)	R
Chilodontidae		
ICN 4993	<i>Chilodus punctatus</i> MÜLLER & TROSCHER 1844	R
Cumiratidae		
ICN 4959	<i>Curimatella alburna</i> (MÜLLER & TROSCHER 1844)**	P
ICN 4141	<i>Curimatopsis macrolepis</i> (STEINDACHNER 1876)	S
ICN 5024	<i>Cyphocharax spiluropsis</i> (EIGENMANN & EIGENMANN 1889)**	P
ICN 4995	<i>Semaprochilodus insignis</i> (JARDINE & SCHOMBURGK, 1841)	P
ICN 4927	<i>Steindachnerina guentheri</i> (EIGENMANN & EIGENMANN 1889)**	P
Erythrinidae		
ICN 4943	<i>Hoplias malabaricus</i> (BLOCH, 1794)	P

Gasteropelecidae		
ICN 4942	<i>Carnegiella strigata</i> (GÜNTHER 1864)	P
Hemiodontidae		
ICN 5013	<i>Hemiodus microlepis</i> KNER, 1858**	R
Lebiasinidae		
ICN 4937	<i>Copella nattereri</i> (STEINDACHNER 1876)**	P
ICN 4964	<i>Nannostomus marginatus</i> EIGENMANN 1909**	P
ICN 4947	<i>Nannostomus trifasciatus</i> STEINDACHNER 1876**	P
ICN 4955	<i>Pyrrhulina laeta</i> (COPE 1872)**	P
Siluriformes		
Asperinidae		
ICN 5286	<i>Bunocephalus</i> cf. <i>coracoideus</i> (COPE, 1874)	A
Auchenipteridae		
ICN 4970	<i>Trachelyopterus galeatus</i> (LINNAEUS 1766)	R
ICN 4983	<i>Centromochlus perugiae</i> STEINDACHNER 1882**	R
Callichthyidae		
ICN 5285	<i>Corydoras rabauti</i> LA MONTE 1941**	A
ICN 4963	<i>Corydoras semiaquilus</i> WEITZMAN 1964**	P
ICN 4951	<i>Hoplosternum littorale</i> (HANCOCK 1828)	A
ICN 4980	<i>Megalechis thoracata</i> (VALENCIENNES 1840)	R
Cetopsidae		
ICN 4938	<i>Pseudocetopsis praecox</i> FERRARIS & BROWN 1991**	S
Loricariidae (Ancistrinae)		
ICN 5583	<i>Ancistrus</i> cf. <i>brevifilis</i> EIGENMANN 1920	R
ICN 4946	<i>Rineloricaria lanceolata</i> (GÜNTHER, 1868)**	R
ICN 5005	<i>Rineloricaria castroi</i> ISBRÜCKER & NIJSSEN, 1984**	R
Loricariidae (Hypostominae)		
ICN 5018	<i>Hypostomus oculeus</i> (FOWLER, 1943)	R
Loricariidae (Loricariinae)		
ICN 4996	<i>Farlowella amazona</i> (GÜNTHER 1864)**	F
ICN 5007	<i>Farlowella oxyrryncha</i> (KNER 1853)	R
ICN 4969	<i>Limatulichthys griseus</i> (EIGENMANN, 1909)**	P
Loricariidae (Hypoptopomatinae)		
ICN 4981	<i>Otocinclus vestitus</i> COPE 1872**	R
Pimelodidae		
ICN 5011	<i>Hemisorubim platyrhynchos</i> (VALENCIENNES 1840)	R
ICN 5022	<i>Heptapterus</i> sp. BLEEKER 1858**	R
ICN 5020	<i>Myoglanis</i> sp. EIGENMANN 1912**	F
ICN 4997	<i>Pimelodella cristata</i> (MÜLLER & TROSCHER 1848)**	F
ICN 5008	<i>Pimelodella geryi</i> HOEDEMAN 1961**	P
ICN 5281	<i>Pimelodus blochii</i> VALENCIENNES 1840	A
ICN 5283	<i>Rhamdia</i> sp. BLEEKER 1858	A
Trichomycteridae		
ICN 4989	<i>Ochmacanthus reinhardtii</i> (STEINDACHNER 1882)**	R
Gymnotiformes		
Gymnotidae		
ICN 5815	<i>Electrophorus electricus</i> (LINNAEUS 1766)	R
ICN 5309	<i>Gymnotus carapo</i> LINNAEUS 1758	R
ICN 4944	<i>Gymnotus pedanopterus</i> MAGO-LECCIA 1994**	R
Hypopomidae		
ICN 4930	<i>Brachyhypopomus beebei</i> (SCHULTZ 1944)**	F

ICN 4925	<i>Hypopygus lepturus</i> HOEDEMAN 1962	P
	Rhamphichthyidae	
ICN 4979	<i>Gymnorhamphichthys rondoni</i> (MIRANDA-RIBEIRO 1920)**	F
	Sternopygidae	
ICN 4972	<i>Eigenmannia virescens</i> (VALENCIENNES 1842)	P
ICN 5006	<i>Sternopygus macrurus</i> (BLOCH & SCHNEIDER 1801)	F
	Cyprinodontiformes	
	Rivulidae	
ICN 5004	<i>Rivulus cf. elongatus</i> FELS & DE RHAM 1981	F
	Beloniformes	
	Belonidae	
ICN 5012	<i>Potamorhaphis guianensis</i> (JARDINE 1843)	P
	Symbranchiformes	
	Synbranchidae	
ICN 4998	<i>Synbranchus marmoratus</i> BLOCH 1795	R
	Perciformes	
	Cichlidae (Cichlasomatinae)	
ICN 5021	<i>Aequidens</i> sp. EIGENMANN & BRAY 1894	R
ICN 4928	<i>Aequidens diadema</i> (HECKEL 1840)	F
ICN 4971	<i>Biotodoma wavrini</i> (GOSSE 1963)**	R
ICN 4929	<i>Bujurquina mariae</i> (EIGENMANN 1922)**	P
ICN 4975	<i>Cichlasoma amazonarum</i> KULLANDER 1983	S
ICN 4926	<i>Heros severus</i> HECKEL 1840	A
ICN 4984	<i>Hypselecara coryphaenoides</i> (HECKEL 1840)**	R
ICN 4933	<i>Pterophyllum scalare</i> (LICHTENSTEIN 1823)	A
	Cichlidae (Geophaginae)	
ICN 4954	<i>Apistogramma bitaeniata</i> PELEGRIN 1936**	P
ICN 4936	<i>Apistogramma cf. ortmani</i> (EIGENMANN 1912)	P
ICN 4958	<i>Satanoperca jurupari</i> (HECKEL 1840)	P
	Cichlidae (Cichlinae)	
ICN 4924	<i>Cichla monoculus</i> SPIX & AGASSIZ 1831	P
ICN 4960	<i>Crenicichla johanna</i> HECKEL 1840	R
ICN 4935	<i>Crenicichla saxatilis</i> (LINNAEUS 1758)	F
	Polycentridae	
ICN 4940	<i>Monocirrhus polyacanthus</i> HECKEL 1840	P

Table 2: Fish species richness in La Arenosa, estimated with different incidence-based richness estimators.

Samples	32
Sobs (Observed species)	109
ICE (Incidence-based Coverage Estimator)	119.39
Chao2 (Incidence based Chao estimator)	115.92
Chao2_SD	4.75
Jack1 (First-order Jackknife estimator)	124.5
Jack1_SD	4.4
Jack2 (First-order Jackknife estimator)	123.17
Bootstrap estimator	117.52

Table 3: Number of fish species reports in different Amazonian *terra firme* forest stream systems.

Area of Study	No. of reported species	Author
La Arenosa Stream, Leticia, Colombian Amazonia	109	This study
3 streams near Manaus, Brazilian Amazonia	53	KNÖPPEL 1970
Streams of the Napo River system, Ecuadorian Amazonia	49	SAUL 1975
Affluent stream of the upper Paraná River, Brazilian Amazonia	19	CASTRO & CASATTI 1997
Streams in the Mamirauá reservation, Brazilian Amazonia	35	CRAMPTON 1999
3 streams of the Urubu River Basin, Amazonas State, Brazil	28	BÜHRNHEIM & COX-FERNANDES 2001

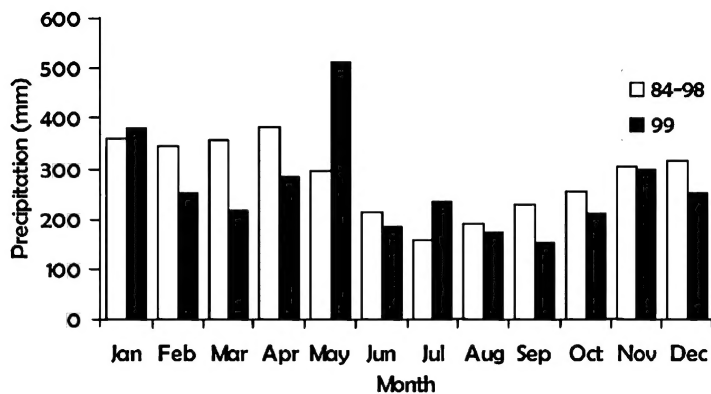


Fig. 1:

Mean monthly precipitation in the area of study near Leticia, Colombia. Values for 1999 and for the 1984-1998 average are shown.

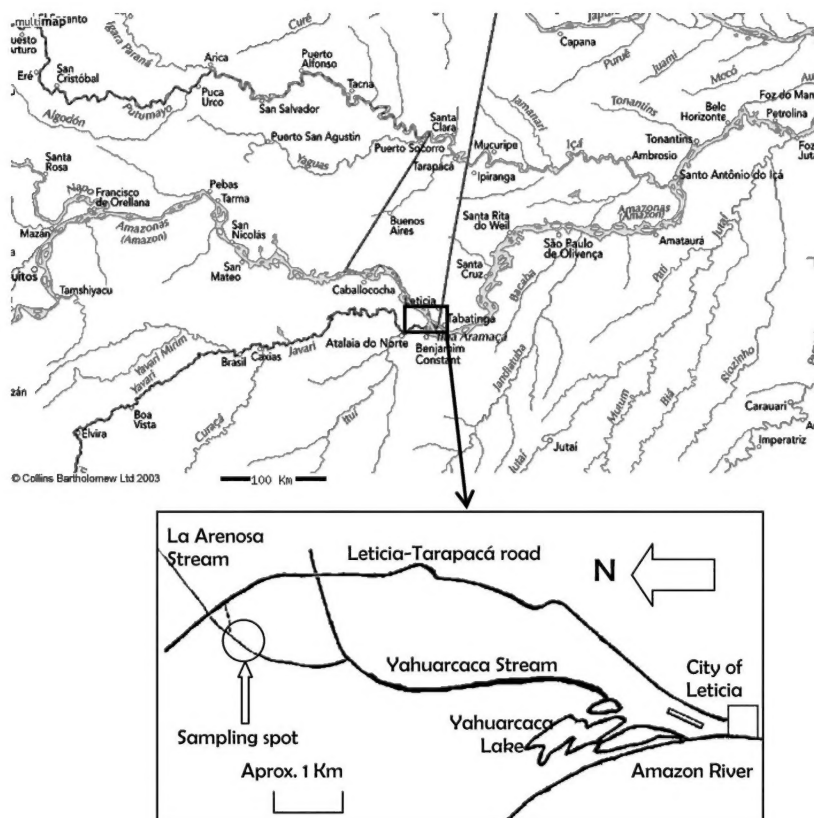


Fig. 2:

Schematic map of the sampling area (map source: www.multimap.com).

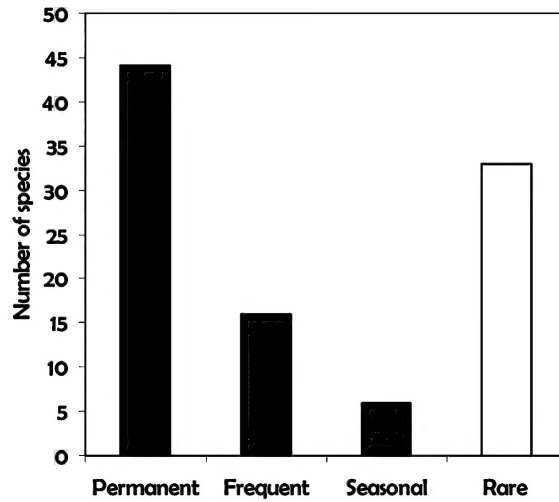


Fig. 3:
Permanency of fish species in La Arenosa during the three major sampling surveys. Permanent, present in the three surveys; Frequent, in two; and Seasonal, in one. Rare species (with one or two individuals) were not included in the permanency analysis.

